

The epiphytic lichen, *Evernia prunastri* L., as a habitat for arthropods: shelter from desiccation, food-limitation and indirect mutualism

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ABSTRACT

On exposed surfaces of tree trunks, the minute structures of the fruticose lichen thalli of *Evernia prunastri* positively influence abundance and living conditions of various corticolous arthropods. The densities of Collembola, Psocoptera and oribatid mites that feed on the lichen's phycobionts are much higher than on the neighbouring bark where algal cover represents the only food resource. The preference for *E. prunastri* is explained by a unique combination of food availability and protection from desiccation in the lichen thalli. Such benefits outweigh the various restrictions placed on grazers by the thalli of *E. prunastri*: solid cortex layers, densely packed and inaccessible, or loose and wind-exposed, lichen branches, cover with sand and detritus, waterfilm after precipitation and the reduced edibility of phycobionts. The balance between such restrictions and the protection afforded to arthropods depends on the thallial growth form. This is a new perspective on primary producers' defence mechanisms. Moreover, for the lichen itself, thallus peripheries of dense growth provide protection from desiccation and wind-adapted growth forms offer optimal shelter from damage by wind. This adaptation is shown to depend on variation in the growth of lichen branches, induced largely by arthropod grazing. Thus, indirect mutualism seems to exist between *E. prunastri* and its grazers under exposed microclimatic conditions.

INTRODUCTION

The trunks of trees are exposed to variation in climatic conditions such as wind, solar radiation and precipitation (Haarlov and Petersen, 1952; Nicolai, 1985, 1986, 1989). The microclimate of epiphytes on the tree trunk, therefore, may be very important for grazing microarthropods. In fact, a correlation has been demonstrated between the degree of epiphyte cover on different orientations of trunk-faces and the species composition and abundance of the corticolous fauna (Pschorn-Walcher and Gunhold, 1957; Travé, 1963; Gjelstrup, 1979; Nicolai, 1985; Büchs, 1988, 1990; Stubbs, 1989; Prinzing, 1997, Chapter 22, this volume). Similar differences might exist between lichens of crust-like and fruticose (shrub-like) growth forms with their correspondingly different microclimates (André, 1983). Other observations of animals that use tree trunks for passage, or for roosting also suggest that orientation/epiphyte cover and weather conditions may be important for arthropod species composition (Bowden *et al.*, 1976; Bauer, 1979; Funke, 1979; J. Adis, personal communication). Until now this complex of biotic and abiotic conditions has been little analysed with regard to arthropod distributional patterns (but see André, 1975; Bauer, 1979).

Solitary tree trunks prove particularly interesting for investigating such epiphytic cryptogams as a habitat for arthropods because of their climatic exposure and species-poor, eurytopic fauna (Pschorn-Walcher and Gunhold, 1957; Travé, 1963). The fruticose lichen *Evernia prunastri* (L.) is a common and conspicuous epiphytic structure found on exposed tree trunks all over Europe, especially in northern Germany (Poelt, 1969; Jacobsen, 1992). This lichen displays an extremely variable growth form and growth density. Morphological observations, comparison of growth forms in different locations and experimental simulation of grazing have shown that such polymorphism is the result of the combined impact of arthropod grazing and microclimate (Prinzing, 1992 and in preparation). The resulting growth forms obviously influence the habitat of corticolous arthropods, sheltering them from solar radiation, wind and rainfall. However, the lichen also displaces *Pleurococcus* algae which are known to be a food source for corticolous arthropods (Jentsch, 1940; Bowden *et al.*, 1976; Bauer, 1979).

In order to study such interactions, the food and climatic requirements of corticolous arthropods were investigated in the laboratory and behavioural reactions to climate were observed in the field. The results were then related to the structural and climatic properties of *E. prunastri* thalli in comparison to bark covered by algae (which is the most common type of epiphyte cover on tree trunks), in order to distinguish which of these microhabitat types better suited microarthropods under different conditions. Suitability for grazers might be important to the lichen itself.

as grazers can induce strong morphological variability in the thalli (for *E. prunastri*, see Prinzing, 1992, also in preparation; for similar fruticose lichen species, see Zopf, 1907; Bachmann, 1929). This feedback effect was also investigated by relating thallial morphology to thallial tolerance to windfall and desiccation.

MATERIALS AND METHODS

Investigations were conducted from August 1991 to February 1992 and in April and May 1992 in the area surrounding Kiel (northern Germany, mostly hilly landscape below 50 m above sea level, oceanic climate). The thalli of *E. prunastri* were investigated two to four times each week at 24 sites on solitary trees or groups of trees at heights from 0.5–2.5 m above the ground. The trees studied were mostly oak (*Quercus robur* L.), as well as lime (*Tilia platyphyllos* Scop., *T. cordata* Mill), ash (*Fraxinus excelsior* L.) and horse-chestnut (*Aesculus hippocastanum* L.). *E. prunastri* thalli were found mainly on north-west- to west-exposed trunk-faces, often in dense stocks. Thallial development and grazing patterns were documented photographically at 3-month intervals at six sites from August 1991 to April 1992.

Distribution and requirements of the arthropods

Arthropod abundance was determined 10 times a week, mainly by 5 minutes of hand-searching of both thalli and bark covered with algae (including bark crevices) using a hand-lens (i.e. time-sampling; Southwood, 1966; Dunger, 1989). Numbers of animals were also determined in 20 thalli of fixed volume (approximately 3 cm³) each week by hand-searching. The drought-tolerance and food requirements of arthropods were determined in the laboratory. The animals were kept at room temperature in plexiglas containers (inner radius 3 cm, height 4 cm). Humidity was supplied from a Petri dish with water put below the gauze floor of the container, avoiding direct water contact on the gauze (Figure 23.1). The containers could be illuminated from below by cold light in order to chase the animals to the shaded upper-side of the substrate (lichen or bark). Feeding behaviour of the animals could then be easily observed from above without further disturbance. To investigate drought tolerance, animals of different species were kept together in the same container without humidification from below.

Structure and climate of the thalli

To characterize the major structural variations of *E. prunastri* under different living conditions, 43 lichen specimens were collected from

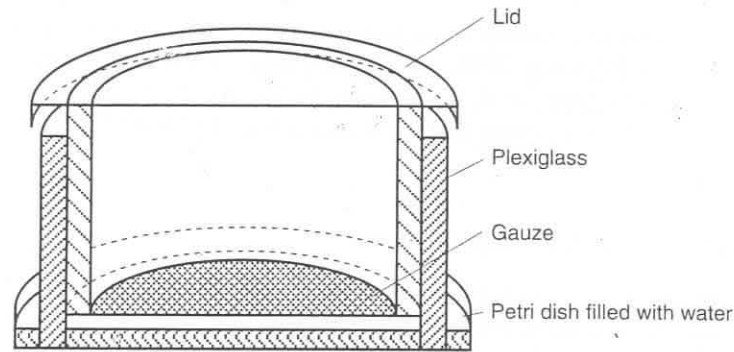


Figure 23.1 Containers for cultivation, observation and experimentation of arthropods, made from two tubes of plexiglass covered by a transparent Petri dish. Base made of gauze and placed in a Petri dish.

different sites on a single oak tree. The following variables were considered: (i) height on the trunk (0.5 and 1.7 m); (ii) exposure to main wind direction (frontal and both lateral trunk faces; no thalli were found on the sheltered face); and (iii) solitary thalli and thalli surrounded by neighbouring *E. prunastri*. At each of the sites differentiated by combinations of these factors, three to four thalli of obviously different growth form were collected. The thalli were cut longitudinally with a razor blade and the proportions of thallus surface with (a) feeding traces, (b) detritus, sand-cover, (c) shelter from wind and sun by outer lichen branches, (d) without dense cover by neighbouring lichen branches and (e) a combination of (c) and (d), were estimated at 10% intervals. The thalli were then sprayed with water three times. After some minutes, when the soaked thalli reached their final form, the proportions of surface were noted with: (i) a cover of waterfilm; (ii) shelter from wind and sun by outer lichen branches; (iii) no dense cover by neighbouring lichen branches; and (iv) both (iii) and (ii).

For measurements of climatic properties of the thalli, 15 intact specimens were each weighed before and after spraying (giving a measure of water uptake capacity), then blow-dried with a hair-dryer from a distance of 30 cm for 1 minute and re-weighed. The ratio of water loss due to drying to the initial water uptake was used as a measure of the wind accessibility of the thalli. A photograph was taken of the front sides of each thallus and used to estimate lichen branch percentage cover (i.e. growth density of frontal thalli) by overlaying transparent graph paper (equivalent to standard quantification of grazing on leaves, for example).

Identifications of lichens and arthropods were made with the aid of reported studies by Wirth (1980) (lichens), Günther (1974) (Psocoptera),

Gisin (1960) (Collembola), Gruner (1976) (Isopoda), Sellnick (1960), Willmann (1931) (Oribatei) and Heimer and Nentwig (1991) (Araneae).

RESULTS

Climatic properties of thalli

Generally, the inner parts of the thalli were sheltered from air flow by the fruticose growth form. This was demonstrated in two different ways. First, the inner, thallial cavities between the branches were hardly penetrated by cigarette smoke blown onto the lichen. Second, after precipitation the central lichen branches stayed moist for hours. This could be easily seen with the naked eye as the thalli of *E. prunastri* and many other lichen species are darker green in colour when wet.

Accessibility to wind (simulated with a hair-dryer) significantly decreased with increasing growth density of the thallus' outer face (Spearman's $R = -0.963$, $P < 0.001$, see Figure 23.2). Optical estimation of the proportion of thalli surfaces that were wind-sheltered confirmed the enormous inter-thallial variability (Figure 23.3(a)). Moreover, movements of lichen branches during soaking by artificial precipitation led to a significant reduction in sheltered areas (Figure 23.3(a)). Both water-uptake during soaking and the extent of cover with a waterfilm also varied markedly between thalli (Figure 23.3(a)).

Arthropods in *E. prunastri* and their requirements

Ten microphyte-grazing arthropod species were regularly found (Table 23.1). Although none of these was restricted to *E. prunastri* alone, large species (such as *Cerobasis guestifalica* (Psocoptera) and species of Entomobryidae) were significantly more common on *E. prunastri* than on bark with algal growth (Table 23.1). Spiders (predominantly juvenile Dictynidae, Linyphiidae and Theridiidae) were also found on *E. prunastri*, mainly in late summer and in autumn.

Artificial wetting of bark induced both Psocoptera and entomobryids to move to the outer surface of the bark, where almost all the algae were growing, and to migrate for long distances. In contrast, Psocoptera and entomobryids living in dry thalli of *E. prunastri* became much less mobile after artificial spraying (Figure 23.4). This basic difference between bark- and thallus-dwelling animals was found in all 15 replicates ($P < 0.001$, sign-test). Similarly, in the laboratory, arthropods were more drought-tolerant when kept in dry, intact *E. prunastri* thalli than on single lichen branches (Table 23.2). Generally, entomobryids were the most sensitive to desiccation and to drowning in a waterfilm, followed by *C. guestifalica* (Table 23.2).

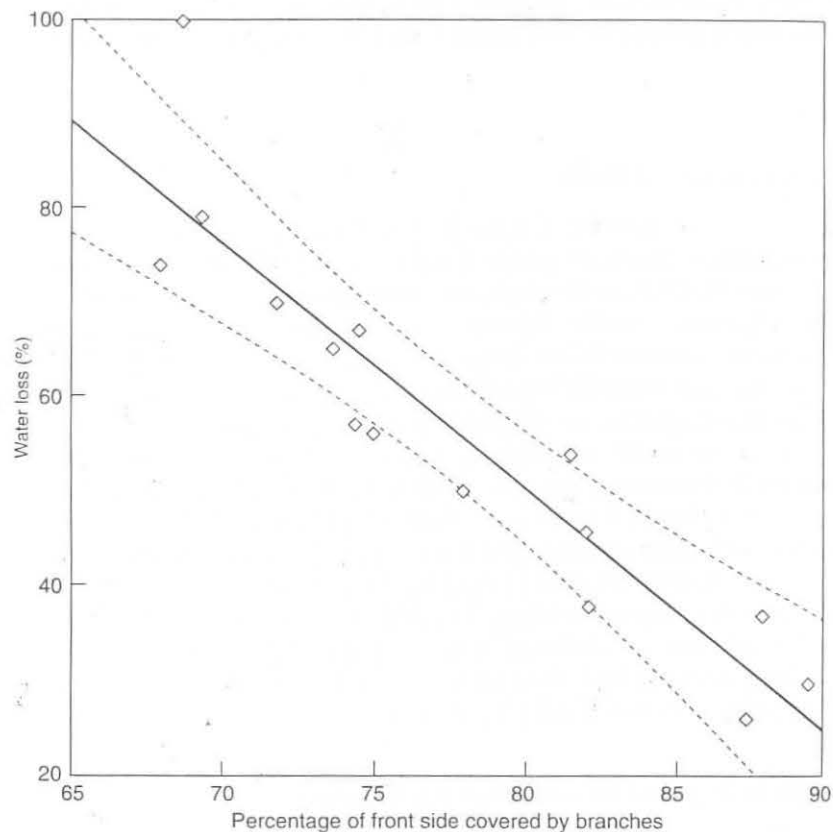


Figure 23.2 Linear correlation between growth density of frontal faces of thalli (percentage of area covered by lichen branches) and accessibility to wind (water loss of soaked thalli due to exposure to a hair-dryer), including 95% confidence limits (Spearman's $R = -0.963$, $n = 15$, $y = -2.58x + 256$).

None of the arthropods was able to feed on all layers of the lichen thallus. The phycobiot layer and algal epibionts were the most frequently grazed. Only *C. guestifalica*, *Orchesella cincta* (Entomobryidae) and oribatids seemed capable of cracking the cortical layer and, thus also feeding on the phycobionts of intact lichen branches (Figure 23.5). *Entomobrya* spp. especially could only graze upon phycobionts which were opened up along the edges by feeding traces of larger grazers or at mechanical ruptures of the cortex layer. Otherwise these species were restricted to grazing on the algal cover of bark and lichens.

Entomobryids, oribatids and *C. guestifalica* were kept alive in the laboratory for up to 5 months when supplied with *Pleurococcus* algae or thalli

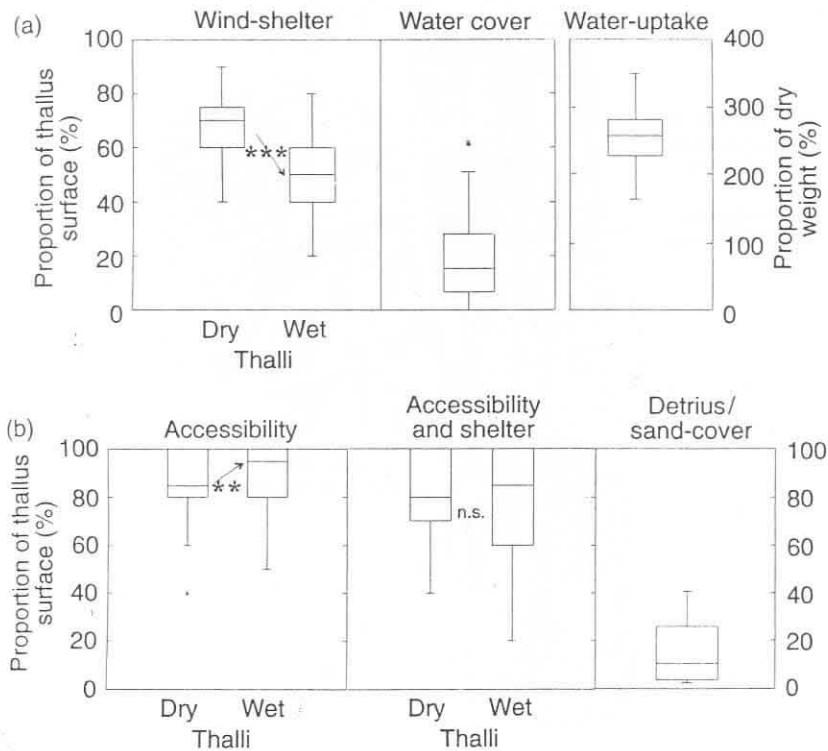


Figure 23.3 Variation of (a) climatic and (b) relevant structural properties on thalli of *E. prunastri* (box-whisker plots with median, outer limits as first and third quartile and exceptional outlying values). Temporal changes due to soaking by artificial precipitation are tested by the Wilcoxon rank test (** and ***, $P < 0.01$ and $P < 0.001$, respectively, n.s. = not significant). For detailed description see text. $n = 43$ thalli, except for water-uptake ($n = 15$).

of *E. prunastri*. Generally, no thallial grazing was found in the field or observed in the laboratory on lichen branches covered by detritus or sand or by the granular lichen, soredia. Furthermore, feeding traces in the thallus' phycobiot layer were rarely found in thalli densely covered by algal epibionts. Correspondingly, in the laboratory, the animals always fed strictly on covers of algal epibionts when presented with a choice. While doing this, the animals were never observed to push and pull with their whole body as they had to when grazing on the thallus itself, especially on its stiff cortex.

Grazing on the cortex and phycobiot layers seemed to be most effective in slightly moistened thalli, whereas in lichen branches with a higher

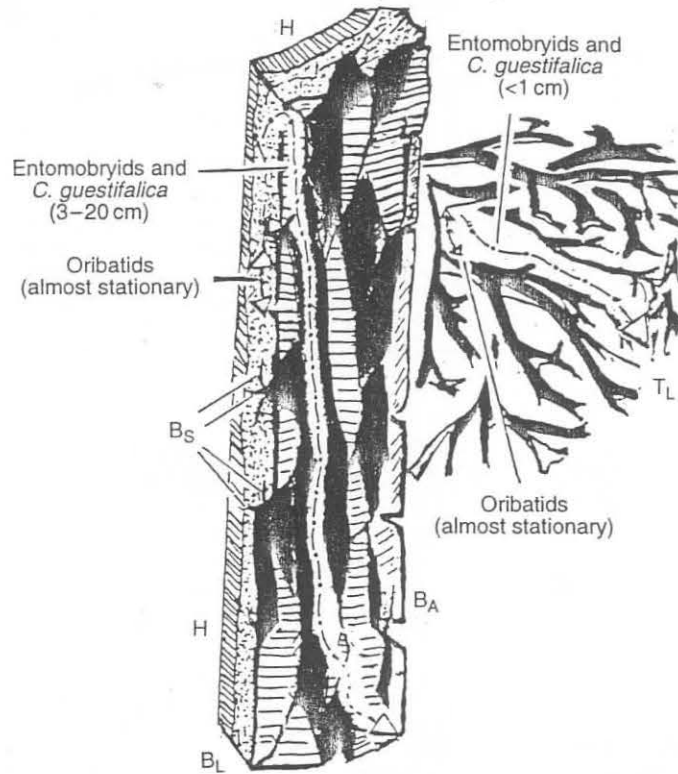


Figure 23.4 Migration distances of arthropods within 10 minutes after moistening thalli and surrounding bark by spraying (during lull conditions, animals stayed stationary with wind intensity of three degrees or more on the Beaufort scale). B_A , upperside of bark covered by algae; B_L , bark in longitudinal section; B_S , bark crevice, mostly free of algae; H , wood; T_L , *E. prunastri* in longitudinal section. Experiments were repeated 15 times (with more than three individuals of entomobryid Collembola, of *Cerobasis guestifalica* (Psocoptera) and of oribatids).

water content the inner cells of the phycobiot layer were avoided (Table 23.3). Correspondingly, in the field after extreme precipitation at the end of September, the majority of feeding traces in all of the 43 collected thalli were covered with such inner phycobiot cells rejected by grazers. During September such restriction of the food resource was probably significant for *C. guestifalica*. Population densities strongly decreased and animals often showed a shortened abdomen (Table 23.1). In the laboratory the only alternative cause of a shortened abdomen was desiccation, which was certainly irrelevant to the above-mentioned field observations. Laboratory observations also showed that oviposition did not result in a shortened abdomen.

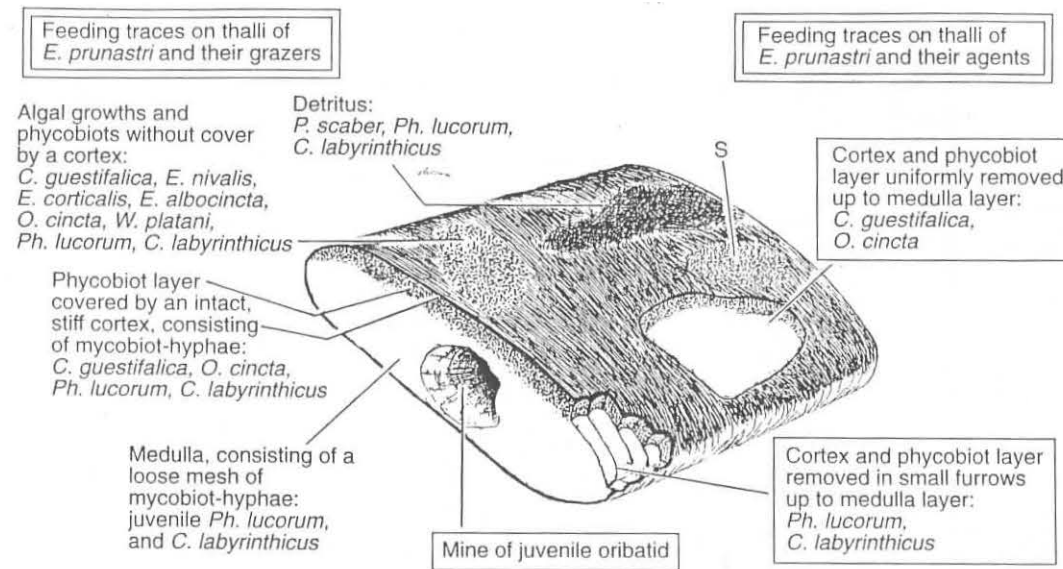


Figure 23.5 Lichen branch of *E. prunastri* as a food source of grazers and the corresponding feeding traces, cross-section from the front, slightly schematic. S, soredia, which are not grazed upon. Full species names are given in Table 23.1.

Table 23.1 Abundance and phenology (except for March) of arthropods found on *Evernia prunastri* and on adjacent bark (including crevices) covered by algae sampled for fixed time-spans or fixed thallial volumes. When animals occurred extremely patchily, the latter number is not given. *Entomobryidae are mainly *Entomobrya nivalis* L., *E. albocincta* Templeton and *Orchesella cincta* L. as well as some *E. corticalis* Nicolet and *Willowsia platani* Nicolet

taxa	abundance		phenology on <i>E. prunastri</i> (months: June–May)
	per 5 min search time on thalli	per app. 3cm ³ thallus volume on bark	
Insecta: Psocoptera <i>Cerobasis</i> <i>guestifalica</i> Kolbe	10–50	max. 4	<div> <div> <div>≤ 7 adults</div> <div>≤ 15 juveniles</div> </div> <div> <div>J J A S O N D J F (M) A M</div> <div> <div>eggs</div> <div>adults</div> <div>juveniles</div> </div> </div> </div> <p>comment: found in all areas of research. Drastic decrease during end of September beginning of October 1991 after the first rainfall that lasted for several days. >50% of the surviving individuals with extremely shortened abdomen.</p>
Collembola: <i>Entomo-</i> <i>bryidae</i> *	2–10	max. 2	<div> <div> <div>≤ 3 adults</div> <div>≤ 5 juveniles</div> </div> <div> <div>J J A S O N D J F (M) A M</div> <div> <div>juveniles and adults of</div> <div><i>Entomobrya spec.</i></div> <div><i>Orchesella cincta</i></div> </div> </div> </div> <p>comment: found on 30 to 80% of investigated trunks, mainly on oaks</p>
<i>Isotoma</i> <i>viridis</i> Bourlet	strongly clustered ≤ 20	(distribution too patchy) > 20	<div> <div>J J A S O N D J F (M) A M</div> <div>juveniles</div> </div> <p>comment: found in large numbers below foliose lichens and bark of oaks and limes throughout the whole year, also as adults</p>
Isopoda: <i>Porcellio</i> <i>scaber</i> Latreille	strongly clustered ≤ 20	" >> 20	<div> <div>J J A S O N D J F (M) A M</div> </div> <p>comment: not found on exposed trees on farmland</p>
Acari: Oribatei: <i>Carabodes</i> <i>labyrinthicus</i> <i>Michael</i> , also <i>Phauloppia luco-</i> <i>rum</i> C.L. Koch	strongly clustered with no obvious differences between bark and lichens (< 40 ind. per thallus)	"	<div> <div>J J A S O N D J F (M) A M</div> </div>

Table 23.2 Tolerance to desiccation and to a waterfilm of common arthropod species on *E. prunastri*. Desiccation experiments were conducted in five containers with four dry lichen branches of *E. prunastri* each, or in five containers with one complete dry thallus of 3 cm³ each, both without water supply. Tolerance is given as survival time in days (d) or hours (h), respectively. Number of animals investigated is given in parentheses. Tolerance to water-cover is measured as the parts of the body that the animals were able to detach from a waterfilm on a thallus (Wp) and as survival time under complete cover of water in hours (Ws, n >10 individuals per species)

	Desiccation		Tolerance to water-cover	
	Dry branches	Dry thallus	Wp	Ws (h)
<i>C. guestifalica</i>	5–7 d (n=20)	10–15 d (n= 24) abdomen shrinks to 2/3 of normal size	Antenna, bristle, often also leg	0.5
<i>O. cincta</i>	4–5 d (n=10)	–	Antenna, bristle	0.5
<i>E. nivalis</i>	2–3 d (n=15)	–	Antenna, bristle	0.5
<i>Ph. lucorum</i> / <i>C. labyrinthicus</i>	5–10 d (n=25)	9–17 d (n=32)	Bristle	>72
<i>P. scaber</i>	3–4 h (n=10)	1 d (n=5)	Whole body	–

Table 23.3 Grazing pattern of phycobiot-feeding arthropods on *E. prunastri* branches of different moisture content (three branches per container and greater than three adults of *Orchesella cincta* (Entomobryidae), four *Cerobasis guestifalica* (Psocoptera), seven *Phauloppia lucorum* (Orabatei), or three *Carabodes labyrinthicus* (Orabatei), respectively

Fraß	Humidity of lichen branches			
	Dry	Slightly	Mediumly moistened	Soaked
Extent	Small patches	Large areas		Patches, by oribatids only
Depth	Cortex + complete phycobiot layer		Cortex + upper phycobiot layer only	
Distribution	Irregular, including edges and tips of branches			

When estimating the extent of feeding traces in the cortex and the phycobiot layer, grazing of >80% of the surface was only found in the peripheries of one out of 43 thalli and in only four of the thalli centres. The centre of the thallus is shaded and therefore less important for the lichen's photosynthesis.

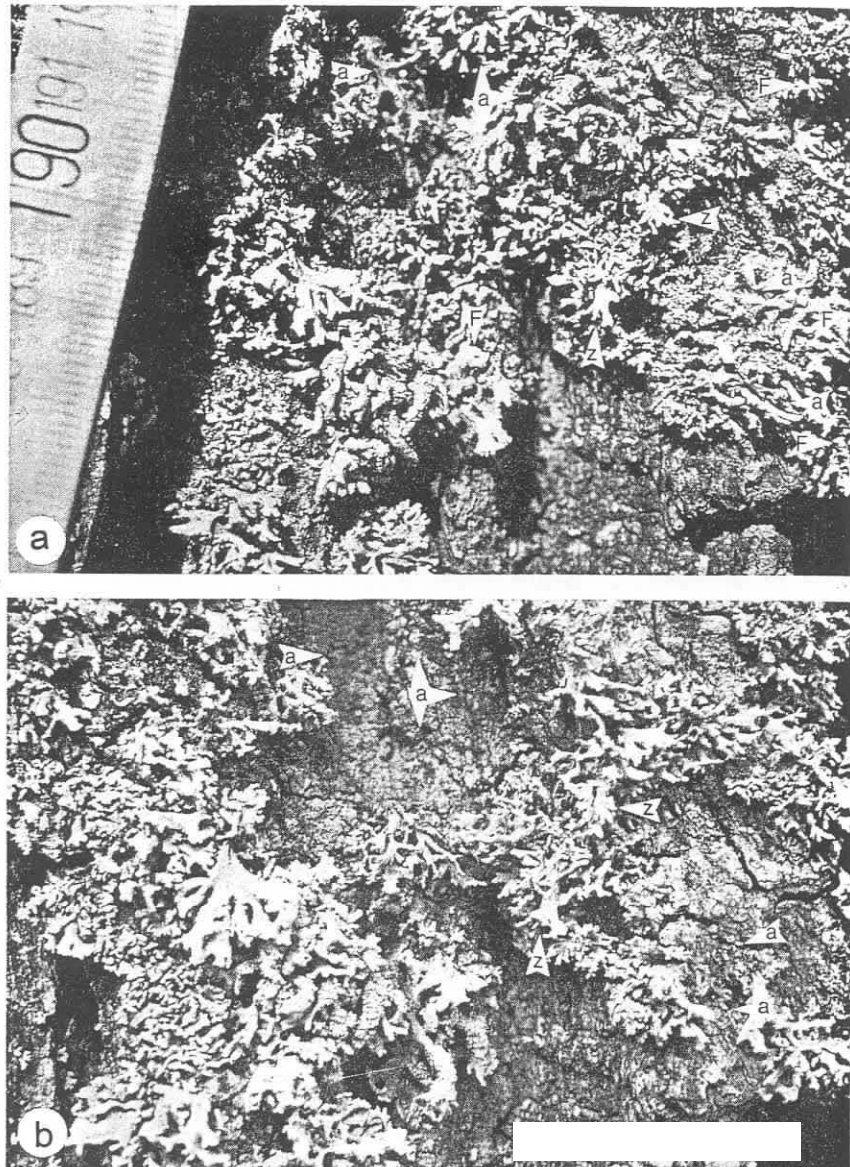


Figure 23.6 Fate of *E. prunastri* thalli on an oak, reflecting the impact of windfall on thalli of different growth patterns between (a) 15 August, 1991 and (b) 22 April, 1992. Lichen branches marked (z) in Figure 23.6(b) were windswept, those marked (a) were even torn off. The latter was also preceded by a windswept stage, as intermediate photographs showed. Such branches were comparatively constant in the growth layer and regular in branching pattern, but they were not more strongly grazed than surviving lichen branches. Feeding traces of *Cerobasis guestifalica* (Psocoptera), *Orchesella cincta* (Entomobryidae) or oribatids were located in comparatively wind-sheltered microsites, recognizable as white patches (marked F) in Figure 23.6(a).

Effect of spatial structure of the thalli on arthropods

Traces of feeding were only found on lichen branches accessible to grazers, but not where there was dense contact with other branches. Feeding was found sometimes on up to 60% of the thallus surface, especially when thalli were dry (Figure 23.3(b)). Proportions of areas both accessible to grazers and sheltered by outer lichen branches varied more between thalli, but were not affected by artificial soaking ($P = 0.860$, Wilcoxon rank test; Figure 23.3(b)).

The grazed portions of the thallus surface were 2.1 times more extensive in central parts of thalli sheltered by outer lichen branches than in the more exposed branches at the periphery of the same thalli ($P < 0.001$, Wilcoxon rank test; e.g. Figure 23.6(a)). In contrast, wind exposure due to the height of thalli on the tree trunks (1.7 m compared with 0.5 m) correlated with a significant increase in the percentage of surface grazed at thallus peripheries ($P = 0.012$, Mann-Whitney U -statistic = 143), whereas grazing was not affected at the thallus centres ($P = 0.417$).

Most feeding traces with intact inner cells of the phycobiot layer (see Table 23.3) were found on the sheltered, central lichen branches, corresponding to the constant, high moisture content. In the thallus peripheries incomplete grazing occurred only after extreme precipitation at the end of September and was then even found in all of the 43 thalli.

Rarely, in very dense thalli, large parts of the surface were covered by detritus and sand which made phycobiotics inaccessible for grazing by arthropods, recognizable by the lack of feeding traces (Figure 23.3(b)).

Effect of thallus growth-form on survival of thalli

During rain, and in particular during stormy weather, thalli from exposed parts of the bark relief were often torn from the trunk. Destruction by other agents such as birds or squirrels was not observed. The destructive impact of wind was also reflected by the windswept shape of thalli before detachment and was recognized in all photographically documented cases (Figure 23.6). In contrast, intact thalli on wind-exposed zones of the trunk showed an aerodynamic dense mesh of lichen branches, some of which even grow back into the bark.

At seven sites near Kiel, 15 to 25 thalli or lichen branches that had fallen from the trunk were collected. All were predominantly constant in growth layers and isotomous-dichotomous in branching pattern in all investigated areas. Moreover, undamaged lichen branches that remained on the trunks were more irregular in growth pattern than the neighbouring detached thalli or branches (observed photographically in 47 out of 52 thalli).

DISCUSSION

E. prunastri as a habitat for grazers: advantages and disadvantages

The results of this study show that thalli of *E. prunastri* are not only an adequate food source for arthropods (even when dry) but also retain humidity and provide shelter from convective desiccation. This protection increases on strongly wind-exposed sites due to an increasing growth density of the lichen (Prinzing, 1992, also in preparation; Zimmer, 1994). Therefore, grazing on the central parts of thalli does not become less intense at the upper, wind-exposed heights of a trunk.

It is possible that grazers also create a humid environment by oxidative synthesis of water from ingested lichen particles. However, in such a case food should eventually become limiting – at least with regard to certain optimally utilized parts of the lichen branches. This was not found to be the case.

Food source and shelter from desiccation within *E. prunastri* could be segregated spatially by distances of not more than several millimetres and, therefore, resources were faster and more flexibly accessible than on bark with algal cover. Effects of the exposure of the whole trunk to wind, sun and rain on the accessibility of different corticolous microhabitats are currently being investigated (Prinzing, 1997, Chapter 22, this volume).

Thalli might also protect grazers from predatory ants, which were observed to be largely unable to climb densely growing thalli of *E. prunastri*. The importance of the above-mentioned advantages of *E. prunastri* as a habitat, compared with bark with algae, is reflected by the greater arthropod density on *E. prunastri*. Nevertheless, even in thalli of *E. prunastri* access to food (mainly consisting of phycobionts) is restricted to some degree, for example by densely packed lichen branches. After soaking, the lichen is less dense, but at the same time the animal's exposure to wind and rain is increased. Moreover, loosely packed, dry lichen branches are especially exposed to desiccation and are correspondingly less grazed. Oribatei are to some extent independent of such restrictions within a thallus, but they are least capable of moving quickly to a favourable microsite.

Even when lichen branches are easily accessible, access to their phycobiont layer is often prevented or complicated by an intact, stiff cortical layer, by a detritus cover, or by inappropriate inner phycobiont cells. The latter two factors depend on the density of thallial growth. The quality of phycobiont cells is also influenced by the actual weather conditions. Overall, these factors help to avoid overgrazing in all regions of a thallus, despite its very low regenerative capacity. Such indirect defence mechanisms are very different from most defence strategies described for

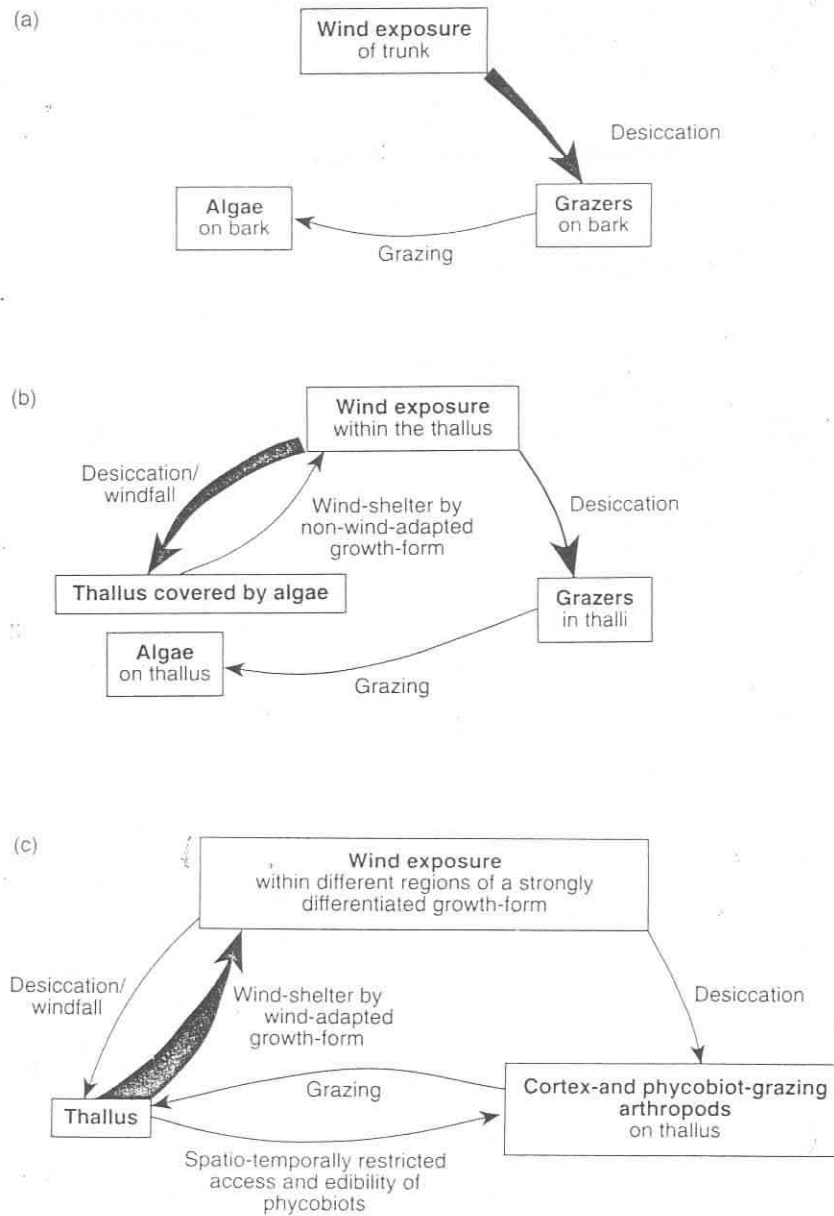


Figure 23.7 Simplified system of interactions between wind-exposure, grazers and (a) algal cover on bark, (b) algal cover on thalli of *E. prunastri* and (c) thalli of *E. prunastri* without algal cover. Only direct effects are presented. Width of arrows represents the probable strength of the effect.

higher plants (Crawley, 1983; Strong *et al.*, 1984; Howe and Westley, 1988). In *E. prunastri*, defence depends strongly on the spatial structure of the polymorphic lichen species, which changes rapidly according to moisture content.

Interactions between *E. prunastri* and grazing arthropods

Grazing by Psocoptera, oribatid mites and *Orchesella cincta* (Entomobryidae) induces variability in the growth of lichen branches. Variable growth of lichen branches is correlated with a low risk of damage by wind, due to the wind-adapted shape of thalli. This shape also restricts desiccation of *E. prunastri*. Therefore, *E. prunastri* does benefit from the activity of the above-mentioned grazers, especially on wind-exposed sites where arthropods most strongly depend on lichen habitat. The direct, detrimental, interactions between grazers and lichen become relatively unimportant. This is supported by the fact that overgrazing of *E. prunastri* was never reported from exposed sites, only from trees in a climatically sheltered forest (Laundon, 1971).

Arthropods and thalli not only inhibit or promote each other, but can also differentiate each others' living conditions (Figure 23.7(a,c)). This effect reaches down to the cellular level of phycobiot layers as a food source and to growth directions of lichen branches following grazing. Strong algal epibiosis on thalli, however, changes the interaction between lichens and grazers (Figure 23.7(b)), as the grazers confine themselves to the more easily accessible algae, thus interrupting most of the mutualistic and regulating feedback mechanisms. Wind damage to such algae-covered thalli is correspondingly high (Prinzing, 1992, also in preparation).

Grazing by *Entomobrya* species does not affect the differentiation and adaptability of thallus growth forms. On the other hand, the means by which the animals feed at the edges of existing feeding traces may hinder the thallus' regeneration, which was often observed to start at that place.

The results presented here might help us to understand the colonization of the canopy layer from arthropod communities on tree trunks. Microarthropod species colonize the canopy layer in a similar fashion to tree trunks and are probably engaged in the same kind of mutualism. Before canopy colonization, however, epiphyte grazers must cross the trunk and use its cryptogam flora.

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